

Widespread regeneration failure of *Persoonia elliptica* (Proteaceae) in the northern Jarrah forest of Western Australia

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Manuscript received August 1987; accepted February 1988

Abstract

Persoonia elliptica R.Br. is a widely distributed but scattered understorey tree of the northern jarrah forest of Western Australia. Stem diameters (at breast height) of 10-30 cm are common but most populations are deficient in trees <10 cm in diameter. The reason for this was studied.

Fruit production is annual and abundant. Although seed viability is high, none could be induced to germinate in laboratory or forest even after physical and chemical treatment. In the forest, the passage of low intensity fire over leaf litter causes abundant germination of dispersed seeds, but few seedlings survive because of browsing by vertebrates, assumed to be kangaroos and wallabies. Height growth of seedlings and lignotuberous seedlings, and diameter growth of trees is slow: we estimate that diameter (breast height) of 10 cm is attained, on average, in c90 years and that recruitment of *P. elliptica* over much of the northern jarrah forest ceased between 1870 and 1904 (95% confidence limits).

A speculative model relating known changes in fire frequency and plausible changes in the abundance of kangaroos and wallabies since permanent European occupation of south western Australia in 1829 is proposed to account for the present stand structure of *P. elliptica*.

Introduction

The failure of regeneration of trees in forests and woodlands has been frequently recognized. Regeneration failure occurs when seedlings fail to attain the size of saplings, giving rise to a population with discontinuous age classes (Jones 1945). Possible causes of regeneration failure include low seed set, excessive predation of seeds before and after dispersal, low seed viability, poor germination, and high mortality of seedlings. However, a major cause is the palatability of seedlings to animals, eg. insects and molluscs (Watt 1923), rabbits (Watt 1919, 1923; Lange & Graham 1983), rodents (Watt 1923, Wardle 1959, Pigott 1969), sheep (Crisp & Lange 1976, Lange & Willcocks 1980, Pigott 1983), goats (Coblentz 1978, Clark & Clark 1981), and kangaroos (Hall, Specht & Eardley 1964). Other factors including temperature, rainfall, or light, have sometimes been implicated (Wardle 1959, 1963a,b, 1978; Hall *et al* 1964; Pigott 1969).

Widespread or chronic regeneration failure has not been reported from natural eucalypt forests and woodlands of Australia, although in some years there may be extensive removal of seeds and fruits by ants and mammals or browsing by mammals (Cunningham 1960, Gilbert 1961, Needham 1960, Statham 1983). Despite this, natural regeneration is usually prompt and adequate.

To ensure impartiality, selection of referees and consideration of their reports was undertaken by Dr N G Marchant at the request of the Hon Editor.

Persoonia elliptica R.Br is an understorey tree of the northern jarrah (*Eucalyptus marginata* Donn ex Smith) forest, attaining maximum height of c7 m and maximum diameter at breast height (130 cm, DBH) of c36 cm. It is widely distributed there (Churchill 1959). For convenience, we recognize four stages in the life of *P. elliptica*: seedlings (plants up to one year old), lignotuberous seedlings (plants >1 yr old but <15 cm tall), saplings (plants 15-130 cm tall) and trees (plants >130 cm tall). Our observations since 1979 throughout the northern jarrah forest have shown that saplings and trees with DBH<10 cm are seldom present although seedlings and lignotuberous seedlings occur in most populations.

In this paper we document the present population structure (frequency of differently sized individuals) of *P. elliptica* and examine factors relevant to explaining the observed failure of regeneration. These include supply and viability of seed, success of germination and establishment of seedlings. Measurements of growth of seedlings and trees are used to estimate when the regeneration failure began. Finally, we speculate about ecological changes that may have been responsible for the regeneration failure.

Population Structure

In this Section, we document the diameter structure of nine populations of *P. elliptica* and provide brief notes about the occurrence of seedlings and lignotuberous seedlings.

Methods

Stands of jarrah forest were chosen mainly on the basis of contrasting rainfall zone and fire and logging history (Table 1). Most were of 15 ha, with one 3 ha (No. 9) and another 125 ha (No. 6). Six of the stands were typical of the northern jarrah forest in that they obviously lacked small diameter trees of *P. elliptica*. Three stands (Nos. 7-9) were chosen because of atypically high representation of saplings and small trees of *P. elliptica*. These three stands were the only ones found by us that had this unusual representation of small trees and saplings.

A complete enumeration of diameter was made in populations where there were fewer than 30 trees; in larger populations only the first 30-50 trees were measured. Diameters were measured over bark at 130 cm above ground level (DBH). The diameter of trees which were forked below, or damaged at breast height, was measured 50 cm or 100 cm above ground level and the DBH calculated from a regression equation relating stem diameter to its height of measurement above ground level. The diameter of the largest stem was measured on trees with several stems growing from the same lignotuber. Saplings were specially searched for and the occurrence of seedlings and lignotuberous seedlings was noted.

Results

In the nine populations studied (Fig. 1), the modal DBH classes were 8-10 cm, 12-14 cm, 16-18 cm, 18-20 cm and 24-26 cm (each once), 10-12 cm (twice) and 14-16 cm (thrice). Populations 1-6 had a structure typical of most of the northern jarrah forest, with a deficiency of DBH classes 0-6 cm and limited representation of DBH classes 6-8 and 8-10 cm. Very few trees in any of the populations had DBH values exceeding 30 cm.

In populations for which complete enumerations of trees were made, density was variable: 0.2 individuals ha⁻¹ (No. 6), c3-4 ha⁻¹ (Nos. 1, 2, 4) and c20 ha⁻¹ (No. 9). The spatial pattern of trees in No. 2 is random, with mean distance between trees of 16 m (Abbott 1984a).

Seedlings and lignotuberous seedlings were found in all populations except Nos. 6 and 8 but seemed to be most abundant in populations 1, 2, 5 and 9, where they were found readily. There was no obvious association between the presence of seedlings and fire and logging history of the forest stands (Table 1, Fig. 1). It is important to record that seedlings and lignotuberous seedlings of *P. elliptica* are very rare in comparison to those of other tree species in the jarrah forest. Saplings were found in populations 7 and 9.

Annual Production and Dispersal of Fruits

In this Section we quantify the phenology of fruit production and consider fruit fall and seed dispersal.

Methods

The presence of fruit on the tree or on the ground beneath the canopy was recorded when trees were measured (in Spring) for DBH (as in the previous section). Detailed observations of flowering times were made in population 2 but casual observations were also made elsewhere. In population 2, five easily accessible branches on each of five trees were marked and the numbers of fruits present counted regularly over two years. In this stand and in population 5, the distance of seedlings from the edge of the canopy of the nearest reproductive tree was measured.

Results and Discussion

Flowering took place in December, and fruits (drupes) attained full size (c17 x 10 mm) by the following May. Many of the immature fruits aborted between March and May. Trees with DBH <11 cm were found not to have ever fruited.

There were large annual differences in the numbers of fruits produced, which were greatest in July 1981 and least in July 1983 (Fig. 2). Most fruit had fallen to the ground by August of each year. All fruit fell beneath the canopy because of the large terminal velocity of the fruit (Abbott 1984a).

Table 1
Characteristics of study areas.

Locality	Grid reference*	Rainfall zone (mm)	Features
1 Ashendon	BN 71.2.9	900-1000	State forest. High quality forest. Cut-over 1914, 1930. **
2 Ashendon	BN 71.2.8	900-1000	State Forest. High quality virgin forest. **
3 Chandler	BQ 69.8.2	1100-1200	State Forest. High quality forest. Cut-over 1890, unburnt since 1937.
4 Mundlimup	BT 63.5.6	1200-1300	State Forest. High quality forest. Cut-over 1872, 1928. **
5 Loc. 990	BT 61.9.8	1200-1300	Reserve. High quality virgin forest. **
6 Yarragil	DD 705.7	1100-1200	State Forest. High quality forest. Cut-over 1933. Near southern edge of range of <i>P. elliptica</i> in the jarrah forest. Unburnt since 1973.
7 Sawyers	AP 72.2.3	900-1000	State Forest. High quality forest. Cut-over 1870s. **
8 Loc. 6203	AM 81.3.9	600-700	Reserve. Low quality virgin forest. **
9 Mt Helena	AN 70.6.9	1000-1100	Private property. Low quality forest, last cut-over c1950 and last burnt 1965.

*CALM 1:50 000 maps (publicly available).

**Fire regime of periodic low intensity (~300 kW m⁻¹) fires since the 1950s.

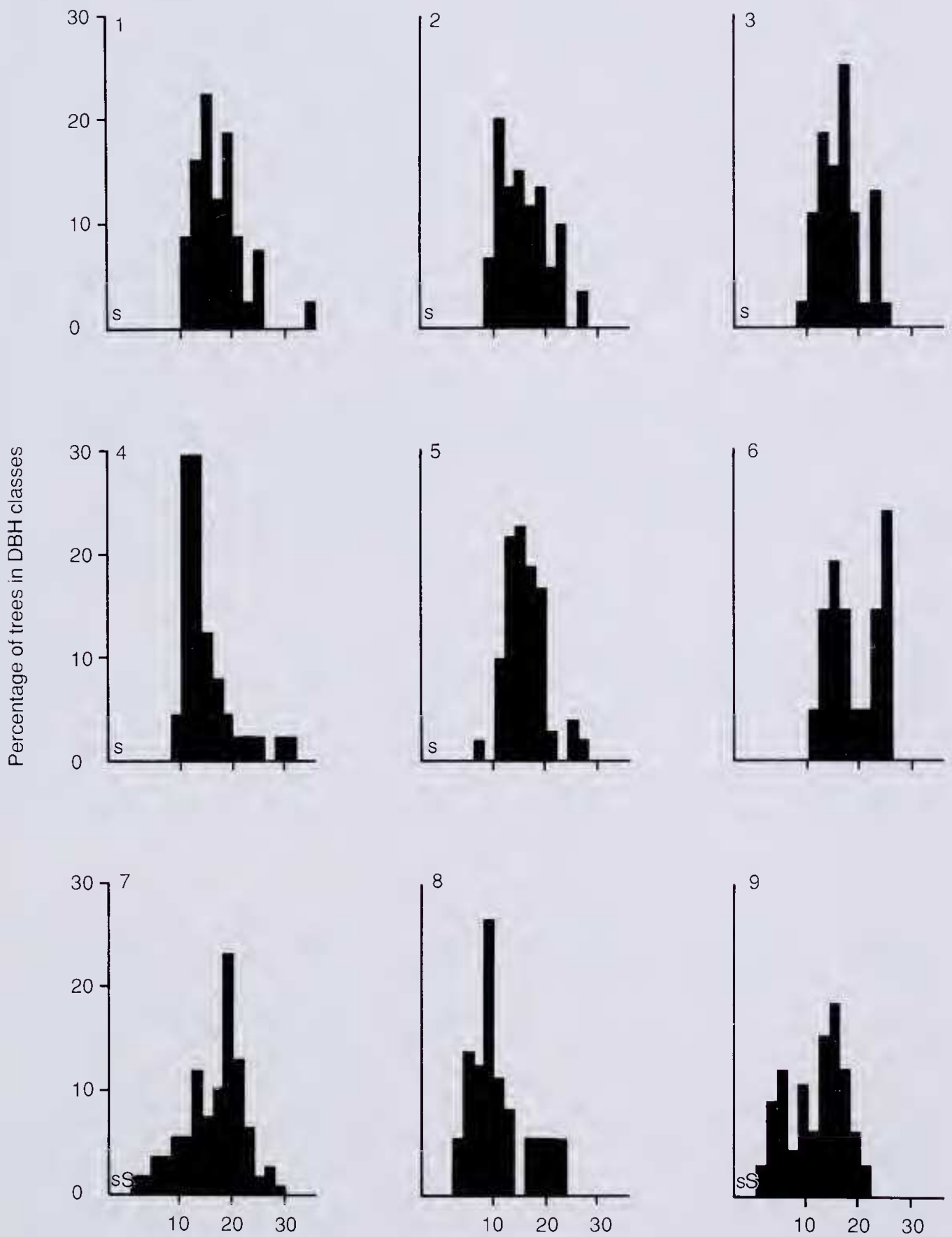


Figure 1 Population structure of *Persoonia elliptica*. Abscissa shows presence of seedlings or lignotuberous seedlings as s, of saplings as S and DBH class, from 0.1-2, 2.1-4 ..., 34.1-36 cm.

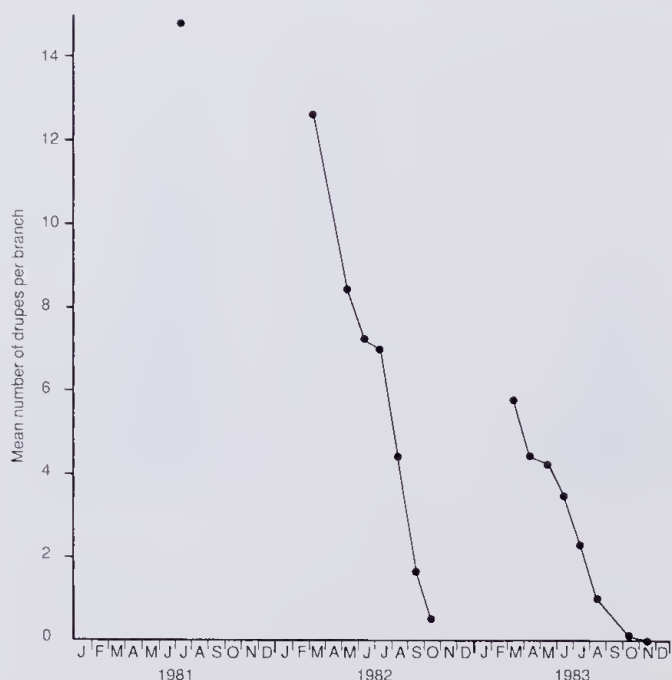


Figure 2 Annual variation in production and shedding of fruit of *Persoonia elliptica* in population 2. One branch of one tree died between October 1982 and March 1983.

Although seeds can be found at any time on the ground beneath the canopy of *P. elliptica*, we have seldom observed seedlings there. For example, in population 2, the mean distance of seedlings from the edge of the canopy of the nearest *P. elliptica* tree was 28.6 m (range 2-66 m, $N = 40$). In population 5, the mean distance was 5.5 m ($N = 44$). In this population the average distance between the bole and the edge of the canopy of the same tree was 2.4 m ($N = 24$).

These data indicate that fruits or seeds are removed from the tree, or from the ground under the tree, or both, by some dispersal agent. Vertebrates rather than invertebrates are responsible (Abbott & Van Heurck 1985). Common Brushtail Possums (*Trichosurus vulpecula*) and Western Brush Wallabies (*Macropus irma*) have been observed to take fruits (S. Davies, pers. comm.). We have also found seed in the faeces of Common Brushtail Possums, Western Grey Kangaroos (*M. fuliginosus*) and Emus (*Dromaius novaehollandiae*). Two common frugivorous birds, the Grey Currawong (*Strepera versicolor*) and the Australian Raven (*Corvus coronoides*), may also eat drupes but we have no direct observations. The fruit is also palatable to humans and may have been eaten by Aborigines.

Viability and Germination of Seed

Here we examine whether the deficiency of trees of *P. elliptica* with diameter <10 cm results from most seeds either being inviable or germinating poorly.

Methods

Viability of seeds with endosperm present was checked with tetrazolium chloride (Colby *et al* 1961).

The following treatments to germinate seeds (collected from beneath the canopies of many trees) were tried:

(a) Seeds were kept at 18°C with full light or 12 hour light/12 hour dark in the laboratory. Part of the sample was then placed on the soil in cages amongst population 2 and kept under observation for two years.

(b) Seeds were soaked in distilled water and then placed in the forest as in (a).

(c) Seeds were kept at 4°C for several weeks and then treated as in (a).

(d) Seeds were filed at both ends to reveal the endosperm and then treated as in (a).

(e) Seeds were boiled in water for 15 minutes and then treated as in (a).

(f) Digestion by birds was simulated by scarifying seeds for 3 hours or treating with acid (as in Glyphis *et al* 1981); seeds were then placed in the forest as in (a).

(g) Seeds were treated with gibberellic acid (method of Bachelard 1967) and then placed in the forest as in (a).

(h) Seeds were placed between hessian sacks (method of Crossland 1981).

(i) Seeds were placed in a small area (1.5 m x 1.5 m) of litter which was then ignited. Seeds were then placed in the forest as in (a).

(j) Seeds from several prolifically fruiting trees in a paddock at Mt Helena were placed in an adjacent fenced enclosure containing a remnant of native vegetation.

(k) Seeds were placed in cages in the forest in various treatments of shading, litter type and depth, and trenching (Abbott 1984b).

(l) Seeds from populations 5 and 9 were placed in cages on the forest floor in population 2.

(m) Fresh drupes were offered to captive emus in order to assess whether passage through the gut facilitated germination.

Results and Discussion

Drupes collected from four populations yielded the following percentage viability: 81% ($N = 52$), 100% ($N = 7$), 73% ($N = 51$) and 48% ($N = 23$). Abbott (1984b) quoted 84% viability for another sample. In all cases there was only one seed per drupe. A sample of 154 seeds collected from under a large *P. elliptica* tree yielded only 7.8% that were obviously damaged by fungi and insects. The presumption is that the remainder were fit for germination.

None of the experimental treatments applied induced seed to germinate, in agreement with Kullman (1981). There is clearly a dormancy mechanism but its precise nature remains unresolved. Our observation (preceding section), that nearly all seedlings are found far from fruiting trees, implicates passage through the gut of vertebrates as the first step in breaking this dormancy.

The emus refused to eat the drupes; it is difficult to introduce new types of food into the diet of captive emus (S. Davies, pers. comm.).

Establishment and Survival of Seedlings

Opportunistic observations made in jarrah forest stands subject to periodic low intensity fire ($<300 \text{ kW m}^{-2}$) in spring showed abundant germination of *P. elliptica* seedlings the following winter. Inspection of these stands more than one year after such fires showed that very few seedlings remained. For example, of 19 seedlings tagged in October 1982 after fire in September 1981 near population 2, only five were alive by February 1983. The other 14 plants had either disappeared or had only their stems remaining, indicating that they had not died because of drought but had died after being browsed. The type of leaf loss was not ascribable to invertebrates but consistent with browsing by vertebrates, probably kangaroos and wallabies. If the seedlings had been killed by drought, their shrivelled remains should have been evident. We therefore designed an experiment to assess the effect of browsing by vertebrates on seedling survival.

Methods

In Chandler Block, 2 km from population 3, a forest stand burnt in spring 1982 was searched in September 1983 for *P. elliptica* seedlings and 49 were located and marked. Twenty were caged (12 mm mesh) and the rest were left as controls. Survival was assessed in November 1983 and March 1984. In August 1981, 14 one year-old seedlings in population 2 were tagged and their survival was checked in August 1982 and August 1983. In September 1981, 41 one year-old seedlings in population 5 were tagged and checked in August of 1982 and 1983.

Results and Discussion

The survival of 6 months-old (November) seedlings differed little between those caged (88.2%) and those uncaged (78.6%). However, after the first summer (March), at 9 months age, there was a significant difference in survival (85% caged, 21% control, $P < 0.05$). Several of the uncaged seedlings showed clear evidence of having been killed by browsing. Because fresh faeces of kangaroos and wallabies (but not of emus) were present, we assume that the first two were responsible. Evidently during the first summer these seedlings are highly palatable to these vertebrates.

After the first year, however, survival of uncaged seedlings is generally high. Of the 14 one year-old seedlings marked in population 2, 13 were still alive one year later and 12 were alive after a further year. Of the 40 one year-old seedlings marked in population 5, 37 were still alive one year later and 35 remained alive after a further year. Hence annual mortality of the seedlings after the first year of life averaged 6.9%. These data suggest that by the second summer the lignotuberous seedling is no longer attractive food for browsing vertebrates.

The apparent contradiction between our observations of abundant germination after fire in the forest and our unsuccessful attempt to germinate seed after an experimental fire ((i), in the previous section) may be explained by assuming that the latter seed had not passed through the gut of a vertebrate. In such a case the seed would still have been dormant. Fire alone is insufficient for germination.

Rate of Growth

Here we examine height growth of seedlings, lignotuberous seedlings and saplings, and diameter growth of trees.

Methods

Rate of growth of seedling, lignotuberous seedlings and saplings was determined from annual measurements of height above ground level. Tree growth was determined from annual measurements of DBH, rather than by counting of growth rings, as these were difficult to discern.

Results and Discussion

Nine months-old seedlings near population 3, caged to prevent browsing, attained a mean height of 5.2 cm (Table 2). Those seedlings 15 months-old (and caged) had achieved a mean height of 6.4 cm (Table 2). Caged plants showed an average annual height increment of 0.2 (range -2 to 1) and 0.6 (range 0-2) cm yr^{-1} in 1981-82 and 1982-83 respectively. Uncaged plants showed an average annual height increment of (-0.4 (range -6 to 4) cm yr^{-1} (Table 2). Thus, as expected, browsing retarded the height growth of those seedlings and lignotuberous seedlings that survived browsing. Uncaged saplings showed an average annual increment in height of 5.9 cm (range 0-14 cm).

Table 2
Growth in height of *Persoonia elliptica*.

Population No. (as in Table 1)	Age (years)	Measured	Height (cm)		N
			Mean	Range	
Seedlings and lignotuberous seedlings					
2	1	Sep 1981*	6.4	3-10	14
2	2	Aug 1982*	6.6	4-11	13
2	3	Aug 1983*	7.2	4-11	12
Near 3	<1	Mar 1984*	5.2	2-7	17
5	2	Aug 1982	6.9	3-10	47
5	3	Aug 1983	6.5	3-10	33
Saplings					
9	?	Sep 1982	62.2	20-120	12
9	?	Sep 1983	68.1	22-130	12

* caged to prevent browsing by vertebrates

Table 3
Growth in diameter at breast height of *Persoonia elliptica*.

Population No. (as in Table 1)	Period	DBH range	Mean	DBH increment (cm yr ⁻¹)		95% confidence interval	N
				Range			
1	Feb 1982-Feb 1983	11.7-25.1	0.12	0-0.4		0.03-0.21	10
1	May 1981-May 1982	15.4-34.7	0.20	0-0.4		0.08-0.32	6
1	Apr 1982-May 1983	10.2-22.8	0.11	0-0.2		0.05-0.17	10
2	Feb 1981-Feb 1982	11.6-25.1	0.03	0-0.1		0-0.06	9
4	May 1981-Apr 1982	7.3-21.3	0.11	0-0.4		0.08-0.14	41
4	Apr 1982-May 1983	7.5-31.7	0.10	0-0.4		0.06-0.14	38
9	Sep 1982-Sep 1983	2.5-23.5	0.14	0-0.6		0.06-0.22	17

Diameter increment of trees, averaged over all populations, was 0.11 cm yr⁻¹, with 95% confidence limits of ± 0.02 (Table 3). Values as high as 0.4 or 0.6 cm yr⁻¹ were sometimes recorded but of the 131 increments measured, 40.5% were zero. We calculate that the average *P. elliptica* tree with DBH of 8, 10, 12 or 20 cm should respectively be 73 years (95% confidence interval of 62-89 years), 91 (77-111) years, 109 (92-133) years or 182 (154-222) years old. That is, establishment took place in 1908 (95% confidence interval of 1892-1919), 1890 (1870-1904), 1872 (1848-1889) or 1799 (1759-1827).

Height and diameter growth is much slower than that of *Banksia grandis* Willd., which is also an understorey tree species of the northern jarrah forest (Abbott 1985).

Effect of Fire on Survival and Growth

Because *P. elliptica* develops a lignotuber (woody swelling at the base of the stem) in the second year of life, typical low intensity fires should rarely kill plants two or more years old. We observed that leaves and shoots are killed by these fires but new shoots resprout from the lignotuber within a few weeks.

Mean height of 3-year old lignotuberous seedlings in population 5 in August 1983 was 6.5 cm (Table 2). A patchy low intensity prescribed fire in spring 1983 killed shoots, but by February 1984 mean height was 4.0 cm (N = 36). A sample of lignotuberous seedlings in unburnt patches had a mean height of 7.0 cm (N = 19). Percentage survival from August 1983 to February 1984 was 100% for the unburnt seedlings and 84% for those burnt.

In other stands, several small trees completely scorched by fire recovered quickly by growing new branches. Many of the larger *P. elliptica* trees in the northern jarrah forest carry fire scars on the lower stem, evidence of their ability to recover from even intense fire.

General Discussion

Three distinct hypotheses can be offered to explain failure in regeneration of a tree species:

- 1 No seed is available;
- 2 Seed is available but is not viable;
- 3 Seed is available and viable but
 - (a) The disperser of the seed has become rare or extinct, (eg. Temple 1977);
 - (b) Extreme climatic events or digestion of seed by a vertebrate are needed to break the dormancy of the seed; or
 - (c) Some relevant ecological process has changed in nature or frequency over the period of interest.

Our data allow rejection of the first two hypotheses. Because seedlings and lignotuberous seedlings can occur well away from the nearest reproductive trees, there is obviously no lack of dispersal agents. We therefore reject hypothesis 3a and the part of hypothesis 3b involving vertebrate digestion. The calculated rate of diameter growth implies that the missing diameter classes <8 cm represent a period of 70-80 years. Local weather records show great variability in annual rainfall over the period 1900-1980 with drought years (eg. 1914, 1940, 1959, 1977) and very wet years (1915, 1917, 1926, 1945, 1955, 1964). Most possible combinations of temperature/rainfall should therefore have occurred during this period and at least one of these should have resulted in massive breaking of dormancy at least once (assuming that these factors are indeed causative). Thus hypothesis 3b is not favoured although difficult to reject with certainty.

Because historical records are incomplete or lacking, it is not easy to define ecological changes that may have occurred over the last 70 years (hypothesis 3c). Using the experimental and observational data collected to identify ecological process(es), we constructed a plausible history of events.

Large quantities of fruit are produced annually by larger trees of *P. elliptica*. The seed has a high viability but has a dormancy period broken effectively by passage through the vertebrate gut. Abundant germination is observed in the winter following a low intensity spring fire. Seedlings are highly palatable to browsing (probably by kangaroos and wallabies) during the first summer and few survive. We therefore identify fire (for germination) and herbivory (causing mortality of seedlings) as the relevant ecological processes affecting regeneration of *P. elliptica*.

How have both processes interacted in the past? We have reliable information about fire (Abbott and Loneragan 1983) but only anecdotes about past densities of kangaroos and wallabies in jarrah forest. The main points of our speculative model are summarized in Fig. 3. We now proceed to the detailed argument.

Before the disappearance of Aborigines from the region in the 1850s, the fire regime in the northern jarrah forest was probably one of frequent, low to moderate intensity fires (Abbott & Loneragan 1983). The density of kangaroos and wallabies should have been relatively low because of hunting pressure from Aborigines and the Dingo *Canis familiaris dingo* (Whitehouse 1977, Abbott 1980). We therefore expect that germination occurred regularly and that seedling survival was high, resulting in abundant recruitment of *P. elliptica*.

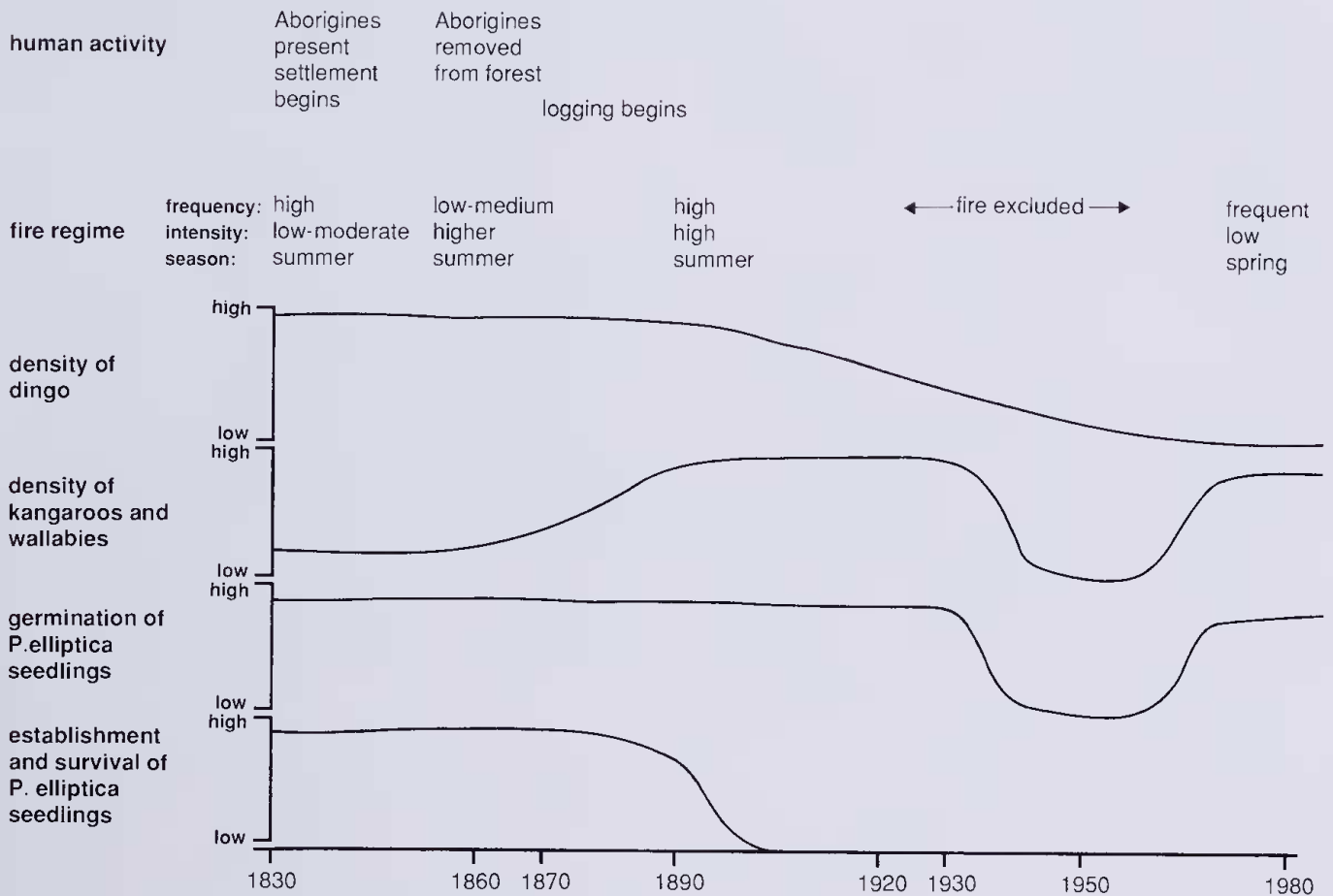


Figure 3 Speculative model relating historical changes in fire regime and hunting pressure by Aborigines to germination and establishment of *Persoonia elliptica*.

Following the disappearance of forest-dwelling Aborigines until the beginning of jarrah logging in the 1870s, the frequency of fires probably declined, resulting in an increase in fire intensity. The density of kangaroos and wallabies should have slowly increased, corresponding to the decrease in numbers of Aborigines (but probably no change in density of the Dingo). Both factors should have resulted in declining recruitment of *P. elliptica*. From the 1870s until the introduction of the Forests Act in 1919, fires once again became frequent because of adjacent agricultural clearing and abundant logging debris on the forest floor. Fires probably also increased in intensity for the same reason. Thus, the increasing length of time without Aboriginal occupation and the intensive farming of land adjacent to the forest (and consequent European trapping of the Dingo because it preyed on sheep) should have allowed densities of kangaroos and wallabies to increase to very high levels, effectively suppressing recruitment of *P. elliptica*. Except as noted below, we do not think that hunting of wallabies and kangaroos by Europeans was of great importance because of the large extent of forest, the long distances between settlements and the small population of Europeans present.

From about 1930 until about 1955, fire was excluded from the northern jarrah forest except for annual burning of 20 m wide firebreaks around 100-200 ha compartments of forest. Such fire exclusion should have reduced the supply of young, nutrient rich plant tissue as food for kangaroos and wallabies, leading to a decline in their numbers. Little recruitment of *P. elliptica* should have occurred in that period. From 1955 to the

present, the northern jarrah forest was again subjected to frequent (5-7 years) low intensity fires. The densities of kangaroos and wallabies were observed to increase following this change in fire policy (J. Havel, pers. comm.) and the density of kangaroos is still relatively high (Short *et al* 1983). Recruitment of *P. elliptica* would have remained low. Although the Dingo in forest areas was replaced by the Fox (*Vulpes vulpes*) by the 1930s, the latter rarely preys on kangaroos and wallabies (Brunner *et al* 1975) and so is not relevant to the ecology of *P. elliptica*.

The ageing of *P. elliptica* on the basis of current diameter growth indicates that, on average, the <10 cm diameter classes represent a period of c90 years, i.e. regeneration began to fail towards the end of the nineteenth century. The virtual absence of trees of DBH <8 cm (equivalent to c70 years age) suggests that recruitment of *P. elliptica* over most of the northern jarrah forest had ceased by about 1910.

How then do we explain the structure of populations 7-9 (Fig. 1) in which trees with DBH <6 cm are relatively well represented? These three populations occur in the extreme north-eastern sector of the northern jarrah forest and have been close to European settlement (farms, orchards, towns) since the 1870s. We suggest that in and around these stands, hunting pressure from Europeans has been relatively high and consistent during the past 100 years. This depressed the population densities of kangaroos and wallabies and allowed some recruitment of *P. elliptica*.

Although the model outlined above is speculative, particularly when compared to the elegant historical study of Peterken and Tubbs (1965), parts of it are testable. The seedlings of *P. elliptica* that have been caged in population 2 and near population 3 should attain DBH of 8 cm within 70-80 years. An index of the abundance of kangaroos and wallabies, based on counts of faecal pellets in various forest stands (Hill 1981) could be correlated with the density of *P. elliptica* seedlings.

Acknowledgments We thank S. Davies for kindly allowing us to study the *Persoonia* population (No. 9) on his property, and for attempting to feed drupes to his captive emus. P. Christensen, S. Davies, J. Havel, O. Loneragan and R. Underwood provided helpful criticism.

References

- Abbott I 1980 Aboriginal man as an exterminator of wallaby and kangaroo populations on islands round Australia. *Oecologia* 44: 347-354.
- Abbott I 1984a Comparisons of spatial pattern, structure, and tree composition between virgin and cut-over jarrah forest in Western Australia. *For Ecol Manage* 9: 101-126.
- Abbott I 1984b Emergence, early survival and growth of seedlings of six tree species in Mediterranean forest of Western Australia. *For Ecol Manage* 9: 51-66.
- Abbott I 1985 Rate of growth of *Banksia grandis* Willd. (Proteaceae) in Western Australian Forest. *Aust J Bot* 33: 381-391.
- Abbott I & Loneragan O 1983 Influence of fire on growth rate, mortality, and butt damage in Mediterranean forest of Western Australia. *For Ecol Manage* 6: 139-153.
- Abbott I & Van Heurck P 1985 Comparison of insects and vertebrates as removers of seed and fruit in a Western Australian forest. *Aust J Ecol* 10: 165-168.
- Bachelard E P 1967 Effects of gibberellic acid, kinetin, and light on the germination of dormant seeds of some eucalypt species. *Aust J Bot* 15: 393-401.
- Brunner H, Lloyd J W & Coman B J 1975 Fox scat analysis in a forest park in south eastern Australia. *Aust Wildl Res* 2: 147-154.
- Churchill D M 1959 The Tertiary and Quaternary vegetation and climate in relation to the living flora in South Western Australia. PhD thesis, Botany Dept, Univ W Aust.
- Clark D A & Clark D B 1981 Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galapagos. *Oecologia* 49: 73-75.
- Coblentz B E 1978 The effects of feral goats (*Capra hircus*) on island ecosystems. *Biol Cons* 13: 279-282.
- Colby V L, Swofford, T F & Moore R P 1961 Tests for germination in the laboratory. *Seeds Yearbook of Agriculture*, 433-443. USDA.
- Crisp M D & Lange R T 1976 Age structure, distribution and survival under grazing of the arid zone shrub *Acacia burkittii*. *Oikos* 27: 86-92.
- Crossland T 1981 Germination of Sandalwood seed. *Ann Rep Mulga Res Centre W Aust Inst Technol, Bentley*, 49-50.
- Cunningham T M 1960 Seed and seedling survival of *Eucalyptus regnans* and the natural regeneration of second-growth stands. *Appita* 13: 124-131.
- Gilbert J M 1961 The effects of browsing by native animals on the establishment of seedlings of *Eucalyptus regnans* in the Florentine Valley, Tasmania. *Aust For* 25: 116-121.
- Glyphis J P, Milton S J & Siegfried W R 1981 Dispersal of *Acacia cyclops* by birds. *Oecologia* 48: 138-141.
- Hall E A A, Specht R L & Eardley C M 1964 Regeneration of the vegetation on Koonamore Vegetation Reserve, 1926-1962. *Aust J Bot* 12: 205-264.
- Hill G J E 1981 A study of grey kangaroo density using pellet counts. *Aust Wildl Res* 8: 237-243.
- Jones E W 1945 The structure and reproduction of the virgin forest of the north temperate zone. *New Phytol* 44: 130-148.
- Kullmann W J 1981 Seed germination records of Western Australian plants. *Kings Park Res Notes* No. 7.
- Lange R T & Graham C R 1983 Rabbits and the failure of regeneration in Australian arid zone *Acacia*. *Aust J Ecol* 8: 377-381.
- Lange R T & Willcocks M C 1980 Experiments on the capacity of present sheep flocks to extinguish some tree populations of the South Australian arid zone. *J Arid Envir* 3: 223-229.
- Needham R J 1960 Problems associated with regeneration of *Eucalyptus gigantea* in the Surrey Hills area. *Appita* 13: 136-140.
- Peterken G F & Tubbs C R 1965 Woodland regeneration in the New Forest, Hampshire, since 1650. *J Appl Ecol* 2: 159-170.
- Pigott C D 1969 The status of *Tilia cordata* and *T. platyphyllos* on the Derbyshire limestone. *J Ecol* 57: 491-504.
- Pigott C D 1983 Regeneration of oak-birch woodland following exclusion of sheep. *J Ecol* 71: 629-646.
- Short J, Caughley G, Grice D & Brown B. 1983 The distribution and abundance of kangaroos in relation to environment in Western Australia. *Aust Wildl Res* 10: 435-451.
- Statham H L 1983 Browsing damage in Tasmanian forest areas and effects of 1080 poisoning. *Bull For Comm Tas* No 7.
- Temple S A 1977 Plant-animal mutualism: coevolution with Dodo leads to near extinction of plant. *Science* 197: 885-886.
- Wardle P 1959 The regeneration of *Fraxinus excelsior* in woods with a field layer of *Mercurialis perennis*. *J Ecol* 47: 483-497.
- Wardle P 1963 Vegetation studies on Secretary Island, Fiordland. Part 5: Population structure and growth of Rimu (*Dacrydium cupressinum*). *N Z J Bot* 1: 208-214.
- Wardle P 1963b The regeneration gap of New Zealand Gymnosperms. *N Z J Bot* 1: 301-315.
- Wardle P 1978 Regeneration status of some New Zealand conifers, with particular reference to *Libocedrus bidwillii* in Westland Natural Park. *N Z J Bot* 16: 471-477.
- Watt A S 1919 On the causes of failure of natural regeneration in British oakwoods. *J Ecol* 7: 173-203.
- Watt A S 1923 On the ecology of British beechwoods with special reference to their regeneration. *J Ecol* 11: 1-48.
- Whitehouse S J O 1977 The diet of the dingo in Western Australia. *Aust Wildl Res* 4: 145-150.